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DOI: <https://doi.org/10.1016/j.neuroimage.2012.01.042>

Posted at the Zurich Open Repository and Archive, University of Zurich

ZORA URL: <https://doi.org/10.5167/uzh-61702>

Journal Article

Accepted Version

Originally published at:

Lehmann, Dietrich; Faber, Pascal L; Tei, Shisei; Pascual-Marqui, Roberto D; Milz, Patricia; Kochi, Kieko (2012). Reduced functional connectivity between cortical sources in five meditation traditions detected with lagged coherence using EEG tomography. *NeuroImage*, 60(2):1574-1586.

DOI: <https://doi.org/10.1016/j.neuroimage.2012.01.042>

Published in: NeuroImage vol. 60, issue 2, pages 1574–1586 (2012).

Reduced functional connectivity between cortical sources in five meditation traditions detected with lagged coherence using EEG tomography.

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Abstract

Brain functional states are established by functional connectivities between brain regions. In experienced meditators (13 Tibetan Buddhists, 15 QiGong, 14 Sahaja Yoga, 14 Ananda Marga Yoga, 15 Zen), 19-channel EEG was recorded before, during and after that meditation exercise which their respective tradition regards as route to the most desirable meditative state. The head surface EEG data were recomputed (sLORETA) into 19 cortical regional source model time series. All 171 functional connectivities between regions were computed as ‘lagged coherence’ for the eight EEG frequency bands (delta through gamma). This analysis removes ambiguities of localization, volume conduction-induced inflation of coherence, and reference-dependence. All significant differences (corrected for multiple testing) between meditation compared to no-task rest before and after meditation showed lower coherence during meditation, in all five traditions and eight (inhibitory as well as excitatory) frequency bands. Conventional coherence between the original head surface EEG time series very predominantly also showed reduced coherence during meditation. The topography of the functional connectivities was examined via PCA-based computation of principal connectivities. When going into and out of meditation, significantly different connectivities revealed clearly different topographies in the delta frequency band and minor differences in the beta-2 band. The globally reduced functional interdependence between brain regions in meditation suggests that interaction between the self process functions is minimized, and that constraints on the self process by other processes are minimized, thereby leading to the subjective experience of non-involvement, detachment and letting go, as well as of all-oneness and dissolution of ego borders during meditation.

Abbreviations: TB, Tibetan Buddhists; QG, QiGong; SY, Sahaja Yoga; AY, Ananda Marga Yoga; ZA, Zen; sLORETA, Standardized Low Resolution Electromagnetic Tomography; PCA, Principal Component Analysis; ROI, Region of Interest; Initial rest, no-task resting before meditation; Final rest, no-task resting after meditation.

1. Introduction

Meditation is currently an important topic in affective and cognitive neuroscience. Many physiological and psychological aspects of meditation practice have been reported applying very different measurement and analysis approaches (e.g. Luders et al., 2009; Lutz et al., 2009; van den Hurk et al., 2010; for an earlier review of the extended literature see Cahn and Polich, 2006).

Brain states of higher cognitive functions such as meditation are implemented as spatially distributed dynamical neuronal networks (Mesulam, 1990; Tononi et al., 1998) that constitute webs of functional connections between brain regions. The brain mechanisms of a functional state are appropriately described by the functional connections between the active brain regions (Singer, 2009). Such descriptions can document characteristic changes between various mental states (e.g. Burgess and Ali, 2002; Mizuhara et al., 2005; Stam, 2000; Walter et al., 1967; White et al., 2009).

The EEG measure of functional connectivity implemented as coherence between head surface recorded EEG time series has been used to assess brain states during meditation. These studies have shown increased EEG coherence during Transcendental Meditation (e.g. Gaylord et al., 1989; Levine, 1976; Travis and Orme-Johnson, 1989; Travis et al., 2002, 2010); experienced practitioners of Transcendental Meditation as well as novices showed increased alpha coherence compared to resting (Dillbeck and Bronson, 1981; Travis, 2001; Travis and Wallace, 1999). Zen meditation reportedly increased alpha coherence in meditation novices (Murata et al., 2004). Sahaja Yoga in long-term meditators produced theta coherence increases between some brain areas but decreases between other areas; in short term meditators, theta coherence only decreased (Aftanas and Golocheikine, 2001). Also, increase of phase locking in gamma frequency during Buddhist meditation has been reported (Lutz et al., 2004) but the authors stressed that phase locking differs from coherence (although both are measures of 'similarity' between pairs of signals measured at two locations, and are thus interpreted as measures of connectivity between the locations).

However, it has been questioned to what extent conventional computation of head surface EEG coherence reveals true functional connectivity between the brain regions under the locations of the recording electrodes because neuronal electric sources do not necessarily project radially to the scalp; computing EEG coherence between intracerebral generator model sources avoids this problem (see also Ruchkin, 2005). Also, the confounding effect of volume conduction in the conventional computation of EEG coherence has been criticized, and omission of zero phase angle coherence values was proposed as remedy (Nolte et al., 2004). Moreover, since the waveform of an EEG time series from a head surface electrode depends on the chosen reference, conventional head surface coherence is reference-dependent (examples in Lehmann et al., 2006).

The present study examines the intracortical functional connectivity of brain electric activity during meditation and during task-free resting preceding and following meditation. The analysis applies 'lagged' coherence that partials out the effect of zero phase angle coherence (Pascual-Marqui, 2007; Pascual-Marqui et al., 2011), thereby removing the volume conduction artifact. Further, it applies the method to cortical time series of electric neuronal generator activity estimated via LORETA-based source modeling of the head surface-recorded EEG data (sLORETA, Pascual-Marqui, 2002) which removes the ambiguity of source localization. Analyzing the source model-generated time series also solves the problem of reference dependence present in the head surface EEG signals. Conventionally computed coherence between the originally recorded head surface EEG time series is reported for comparison.

There are obvious differences between meditation traditions and meditation techniques. Considering these differences, taxonomies of meditation techniques have been proposed (e.g. Fischer, 1971; Lutz et al., 2008; Mikulas, 1990; Travis and Shear, 2010; distinctions were emphasized by Kabat-Zinn, 1982). Data available to us for the present study were from experienced practitioners of five different meditation traditions: Tibetan Buddhism, QiGong, Sahaja Yoga, Ananda Marga Yoga, and Zen. The meditators were recorded while performing that meditation exercise which their respective tradition regards as the route to the most desirable meditative state; recordings during no-task resting before and after meditation were also done. Because of the obvious differences between meditation traditions, the data from each of the five groups were analyzed separately.

On the other hand, apparently there are common goals resulting in common subjective experiences of the meditation practices across schools and traditions (Brewer et al., 2011; Cahn and Polich, 2006; Fischer, 1971; Goleman, 1996; Hinterberger et al., 2011; Kabat-Zinn, 1990; Walsh, 1982): The handling of the contents of consciousness (avoiding intruding unintended thoughts as described in terms such as e.g. letting go, benevolent disregard, detachment), and the quality of the conscious self-awareness (attaining a pleasant, peaceful state of mind as described in terms such as all-oneness, bliss, oceanic feeling, transcending, expanded consciousness).

The present study separately analyzed each of the five groups in order to examine how brain electric functional connectivities differ between resting and meditation, and whether changes into and out of meditation are compensatory. Analyzing the brain activity of meditators from different traditions resulted in the surprising finding that the optimal meditation state in all the five traditions is characterized by reduced intracortical functional connectivity compared to no-task resting.

2. Methods

2.1. Participants

We analyzed EEG data from five groups of experienced meditators that were available to us. The meditators belonged to different meditation traditions: 13 Tibetan Buddhists (TB), 15 QiGong practitioners (QG), 14 Sahaja Yoga practitioners (SY), 14 Ananda Marga Yoga practitioners (AY) and 15 Zen practitioners (ZA). The study was approved by the Ethics Committee of the Tokyo University Medical School (#1364) for the TB, QG, SY and AY, and by the Ethics Committee of the University Hospital Zurich for the ZA. The participants were fully informed about the goal and methods of the study, and gave their written consent.

Gender, and mean years of age, and mean years of meditation experience (we asked for the year when the meditator had started practicing meditation everyday) with standard errors and ranges of the meditators of the five traditions are listed in Table 1. All participants used their right hands for writing. The participants had no history of head trauma or mental diseases, did not take centrally active medication and were not drug users.

Table 1.

Demographics of the meditators of the five traditions (groups).

	Number		Years of age				Years of meditation experience			
	total	men	mean	SEM	max	min	mean	SEM	max	min
Tibetan Buddhists	13	13	38.9	2.3	58	27	12.2	1.9	25	1
QiGong	15	15	37.2	2.0	49	25	6.6	0.9	13	2
Sahaja Yoga	14	4	43.9	2.7	63	26	8.5	1.6	20	1
Ananda Marga Yoga	14	9	45.2	2.1	56	31	16.9	2.4	33	5
Zen	15	9	42.0	2.0	56	29	12.3	1.4	21	5

The TB were Lamas from Tibet and India, from the Nyingmapa and Kagyupa traditions, who temporarily stayed in Taipei for missionary work; they meditate daily for at least 60 minutes. The QG were Taiwanese lay people who studied under Qigong Master Feng-San Lee at Taipei; they meditate daily for at least 45 minutes. The SY were Taiwanese lay people who meditate daily for at least 30 minutes; the AY were westerner and Hindu monks and nuns who live in Taipei; they meditate daily at least for 2 hours; the ZA were Swiss lay people who regularly participate in meditation exercises at the Zen Dojo Zurich, a Soto Zen institution; they meditate daily for at least 60 minutes. The meditators of all five groups have the habit to participate occasionally in retreats.

TB were paid 1000 NT\$/person; QG, SY and AY were unpaid volunteers; ZA were paid 40 CHF/person.

2.2. Recording

The EEG recordings of TB, QG, SY and AY were done at the EEG Laboratory of the Department of Neurology, General Veterans Hospital in Taipei, during September-December 2006. The EEG was recorded versus combined ears (the 19 standard EEG channels of the international 10/20 system were analyzed), together with eye movement, muscle and ECG channels, using silver/silver-chloride electrodes with the Hospital's 32-channel Nicolet Voyager Digital EEG system; EEG was band passed from 1 to 70 Hz and digitized at 256 samples/s.

The EEG recordings of ZA were done at the KEY Laboratory at the University Hospital of Psychiatry in Zurich, using a 64-channel M&I system (Prague, Czech Republic), 58 electrodes were attached (Easycap System Munich, Germany) at locations of the international 10–10 system (Nuwer et al., 1998) with 2 additional channels for eye movement recordings. EEG was band-passed from 0.5 to 125 Hz and digitized at 250 samples/s, off-line up-sampled to 256 samples/s.

2.3. Protocol

The protocol comprised 6 sequential recording conditions, but only conditions 1, 3 and 4 were done in all five groups:

1- Initial resting: 20 s eyes opened, 40 s eyes closed; 4 cycles. TB, SY, and AY: lotus position, QG: sitting on stool, ZA: sitting on chair with armrests. For TB, QG, SY and AY, experimenters aimed at obtaining at least 20 s of artifact-free data and therefore often extended the planned eyes-closed recording times, but no more than the first 160 s of artifact-free data were used. The ZA recordings exactly followed the protocol.

2- Breath counting (not used in present analysis) only in TB, QG, SY and AY: 5 minutes. Participants were asked to silently count their inspirations from 1 to 10, continually repeating this sequence during the entire 5 minutes.

3- Meditation (described below): TB, QG, SY, and AY: 20 min, ZA: 60 min.

4- Final resting: see initial resting.

5- Mental arithmetic (not used in present analysis) only in QG, SY, and AY: 5 minutes, participants were asked to continually subtract 7, starting from 1000, and restarting from 1000 if zero was reached or track of calculation was lost.

6- Post arithmetic resting (not used in present analysis) only in QG, SY, and AY: see initial resting.

In sum, conditions 1 (initial resting), 3 (meditation) and 4 (final resting) were done in all five participating groups; these three conditions were used in the present analysis.

2.4. Meditation

Position: TB, SY, AY, and ZA: sitting in lotus position; QG: sitting on a stool.

Eyes: TB, QG, SY, and AY: eyes closed; ZA: eyes half closed, facing the wall at a distance of about 1 meter.

The meditation practices in the five traditions that lead to optimal meditation states were, in keywords (selected from descriptions given by the representative of each group):

TB: dissolution into Buddha, letting thoughts pass by, reaching mental emptiness, ego-dissolution.

QG: diminution of spontaneous thoughts, reaching higher sensory awareness, immersing in 'Qigong' (gentle slow arm movements in synchrony with breathing), transcending.

SY: self realization, growth of self awareness, thoughtless awareness.

AY: withdrawal of the senses, transcendence into pure, limitless supreme consciousness.

ZA: just sitting, letting phenomena arise and pass, objectless concentration, not thinking.

2.5. Data Conditioning

Eye movement artifacts were corrected using independent component analysis. Then, all data were parsed into data epochs of 2 seconds. All data epochs were screened for artifacts by hand-and-eye on a PC display. Data epochs containing movement, sweat, muscle and technical artifacts were omitted. Up to 3 bad channels were replaced by the average of the direct neighbor channels. In the five groups, on average across participants, N/N channels were replaced: TB: 1.5/19, QG: 1.4/19, SY: 0.5/19, AY: 0.3/19, ZA: 1.0/58. If there were more than 3 bad channels, the subject was excluded (1 TB, 1 ZA). From all data sets, the 19 standard channels (Fp1/2, F7/8, F3/4, Fz, T3/4, C3/4, Cz, T5/6, P3/4, Pz, O1/2) of the international 10–20 system were selected for further analysis.

The artifact-free EEG data eventually available for analysis is listed in Table 2.

Table 2.

Artifact-free EEG data (s, mean and its standard error (SEM) across participants) eventually available for analysis.

	Initial rest		Meditation		Final rest	
	mean	SEM	mean	SEM	mean	SEM
	s	s	s	s	s	s
Tibetan Buddhists	153.4	3.3	1116.0	55.4	139.8	9.9
QiGong	144.9	4.3	1006.8	45.7	141.7	2.5
Sahaja Yoga	142.7	4.9	1102.9	13.7	146.3	6.2
Ananda Marga Yoga	144.7	4.2	1041.9	36.9	153.0	2.1
Zen	120.2	2.3	1622.6	87.1	118.0	4.2

2.6. Coherence

2.6.1. Intracortical LORETA-based lagged coherence

All EEG data epochs were re-computed into cortical current density time series at 6239 cortical voxels using standardized Low Resolution Electromagnetic Tomography (sLORETA, Pascual-Marqui, 2002), available as free academic software package at <http://www.uzh.ch/keyinst/NewLORETA/LORETA01.htm>.

The sLORETA method is a properly standardized discrete, linear, minimum norm, inverse solution that solves the problem to compute the three-dimensional cortical distribution of the electric neuronal source activity from the EEG measurements which are recorded on the head surface. The particular form of standardization used in sLORETA endows the tomography with the property of exact localization to test point sources, yielding images of standardized current density with exact localization, albeit with low spatial resolution (i.e. neighboring neuronal sources will be highly correlated). The detailed description of the method can be found in (Pascual-Marqui, 2002). The proof of its exact, zero-error localization property is given in (Pascual-Marqui, 2009), where it is also shown that sLORETA has no localization bias even in the presence of measurement and biological noise. In this sense, sLORETA is an improvement over the previously developed related tomography LORETA (Pascual-Marqui, 2002). Validation for sLORETA tomography mostly rests upon the abundant published validation for the previous LORETA method. For instance, excellent localization agreement has been reported in multimodal imaging studies with functional MRI (Mulert et al., 2004; Vitacco et al., 2002), structural MRI (Worrell et al., 2000), and PET (e.g. Dierks et al., 2000; Zumsteg et al., 2005). Further validation based on accepting as “ground truth” the information provided by intracranial recordings in humans has been reported in a number of papers (e.g. Yang et al., 2011; Zumsteg et al., 2006). Several recent papers also documented that sLORETA reveals valid results (e.g. Betting et al., 2010; Dümpelmann et al., in press; Laxton et al., 2010). Particularly noteworthy is a comparative validation study using intracranial recordings from epilepsy patients (Plummer et al., 2010) where they show that overall, sLORETA is the method with lowest localization error.

Regions of Interest (ROIs) are needed for the estimation of electric neuronal activity that is used to analyze brain functional connectivity. No general rules for constructing the ROIs are available. In order to assess functional connectivity between all major areas, the cortex areas under the 19 head surface electrode locations Fp1/2, F7/8, F3/4, Fz, C3/4, Cz, T3/T4,

T5/6, P3/4, Pz, O1/2 of the international 10/20 system (Jasper, 1958) were used. The brain regions under these electrodes are tabulated in (Okamoto et al., 2004). A ROI was defined for the cortical voxels under each electrode, in such a way that all cortical voxels were assigned to the "origin" electrode to which they were closest. The signal at each cortical ROI consisted of the average electric neuronal activities of all voxels belonging to that ROI, as computed with sLORETA. Between the sLORETA current density time series of the 19 ROIs, intracortical 'lagged' coherence (Pascual-Marqui, 2007; Pascual-Marqui et al., 2011) was computed between all possible 171 pairs of the 19 ROIs for each of the eight independent EEG frequency bands (Kubicki et al., 1979; Niedermeyer and Lopes da Silva, 2005 p. 1234) of delta (1.5-6 Hz), theta (6.5-8 Hz), alpha-1 (8.5-10 Hz), alpha-2: (10.5-12 Hz), beta-1 (12.5-18 Hz), beta-2 (18.5-21 Hz), beta-3 (21.5-30 Hz), and additionally gamma (35–44 Hz) for each subject and for each condition.

The well known definition for the complex valued coherence (see e.g. Nolte et al., 2004) between time series x and y in the frequency band ω is:

$$r_{xy\omega} = \frac{\text{Re Cov}(x, y) + i \text{Im Cov}(x, y)}{\sqrt{\text{Var}(x) \times \text{Var}(y)}} \quad (1)$$

which is based on the cross-spectrum given by the covariance and variances of the signals, and where i is the imaginary unit ($\sqrt{-1}$). The squared modulus of the coherence is:

$$r_{xy\omega}^2 = \frac{[\text{Re Cov}(x, y)]^2 + [\text{Im Cov}(x, y)]^2}{\text{Var}(x) \times \text{Var}(y)} \quad (2)$$

and the lagged coherence (Pascual-Marqui, 2007; Pascual-Marqui et al., 2011) is:

$$\text{Lag}R_{xy\omega}^2 = \frac{[\text{Im Cov}(x, y)]^2}{\text{Var}(x) \times \text{Var}(y) - [\text{Re Cov}(x, y)]^2} \quad (3)$$

The lagged coherence was developed as a measure of true physiological connectivity not affected by volume conduction and low spatial resolution. It has been shown in Pascual-Marqui et al. (2011) to give an improved connectivity measure as compared to the imaginary coherence proposed by Nolte et al. (2004).

2.6.2. Head surface EEG coherence

After re-computation of the EEG data to average reference, classical coherence (Eq. (2)) was computed between all possible 171 pairs of the 19 electrode locations for each of the eight independent EEG frequency bands (see preceding Section 2.6.1) for each subject and for each condition.

2.6.3. *Statistical analysis of coherences*

The intracortical lagged coherence results between the 19 ROIs, and the conventional EEG coherence results between the 19 head surface locations were analyzed as follows:

For each group of meditators and for each EEG frequency band, using paired t-statistics on the coherence values after Fisher's z transformation, the 171 possible coherences were compared between meditation versus initial rest as well as meditation versus final rest. Correction of significance for multiple testing applied the nonparametric randomization procedure (Nichols and Holmes, 2002) in the sLORETA program package. The correction was computed for the two comparisons between conditions for each frequency band for each group.

2.7. *Topography of the principal functional connectivity*

The major spatial tendency common to all significant functional connectivities (resulting from the comparisons between conditions) between the 19 ROIs of a given group, now called 'principal functional connectivity' was computed using principal component analysis as follows (see Fig. 1): All significant connectivities, i.e. connected pairs of original locations were centered to the origin of a 3-D space by subtracting for each pair the mean location of the pair (Fig. 1A). The first principal component was computed for all participating location pairs (connectivities) yielding a straight line in three-dimensional result space (Fig. 1A4). All connectivities were normalized to unity sphere. The two pair locations of each connectivity were orthogonally projected onto the principal component straight line (Fig. 1B). The projected location was labeled 'A' if the distance of the resulting point to the origin was positive and the corresponding location of the pair was labeled 'B'. The original threedimensional pair locations of the participating connectivities, now labeled as A and B, were separately averaged for A's and B's into x, y, z mean locations (and standard errors) for each group, thus constituting a principal functional connectivity for a given group, for a given frequency band, and for a given comparison between conditions (Fig. 1C).

In a subsequent, second principal component analysis (done as above), the principal functional connectivities of the five groups were computed into a principal functional connectivity for a given frequency band and a given comparison between conditions.

A repeated measure ANOVA (2 comparisons between conditions \times those frequency bands that yielded significant differences between conditions in all five groups \times 2 mean locations: A and B \times 3 brain axes: x, y, z) was done on the topographies of the principal functional connectivities of the five groups. All mean locations A and B of the principal functional connectivities were planned to be tested on the three brain axes for possible differences between the two comparisons between conditions.

2.8. *Power spectra*

Power spectra were computed from the head surface EEG data versus average reference using an FFT routine with box-car windowing. The spectra were subject-wise normalized ('relative power') and averaged across the 19 channels for each subject and condition. Integrated values were computed for the eight independent frequency bands of delta through gamma (see Section 2.6.1. above).

3. Results

3.1. Lagged coherence between intracortical ROIs

Lagged intracortical coherences that differed at $p < 0.05$ after correction for multiple testing between meditation and initial rest or between meditation and final rest were identified. The t -values accepted at $p < 0.05$ after correction for multiple testing ranged from 4.811 to 5.383. All significant differences of lagged intracortical coherence between conditions concerned lower values during meditation than initial or final rest, i.e., none of the tests reached significance for higher values during meditation than initial or final rest in any frequency band. The total number of significant cases in all eight frequency bands in the five groups were: 49 for TB, 138 for QG, 106 for SY, 33 for AY and 33 for ZA, respectively. The five groups markedly differed in the number of significant cases in given frequency bands (Fig. 2A and B).

We note that for the comparison between initial rest versus meditation (Fig. 2A) as well as for the comparison between final rest versus meditation (Fig. 2B), the two frequency bands of delta and beta-2 showed one or more than one significant difference in all five groups. On the other hand, Fig. 2C shows that the results differed somewhat between initial rest versus meditation and final rest versus meditation. This latter Figure also shows that the greatest numbers of significantly lower lagged intracortical coherence during meditation, comparing both initial rest versus meditation as well as final rest versus meditation, were observed for the frequency bands of delta and beta-2.

Fig. 2D displays the grand means across groups and comparisons for each frequency band of the number of tests that were significant after correction for multiple testing; the standard error bars show a relatively large variance across groups in the delta band and a small variance in the beta-2 band.

3.2. Topography of the principal functional connectivity between intracortical ROIs

To test the topography of the connectivities for common tendencies across groups, the results of the delta and beta-2 frequency band were suitable since all five groups are represented with significant results in these two frequency bands. The connectivities that after correction for multiple testing significantly differed between conditions in the delta and beta-2 frequency bands are illustrated in Fig. 3 which shows the concerned connections between the 19 ROIs in glass brain view seen from above. In some cases where there are not too many connections, a predominant topography can be gleaned from examining the display. For example, in the delta band, visual inspection suggests that in the comparison of final rest versus meditation (Fig. 3, Delta f-R) there is a general tendency for left to right-oriented connections in posterior regions in the TB group, and a general tendency to anterior left to more posterior right-oriented connections in the AY group. When many connections are involved as e.g. in the QG group, such guesses evidently become impossible.

The computation of the topography of the principal functional connectivity allows further evaluation without subjective decisions. The principal functional connectivities obtained from the connectivities of Fig. 3 are displayed in Fig. 4. Inspection of these results suggests in turn that in both frequency bands, the principal functional connectivities differ between initial rest versus meditation and final rest versus meditation, and differ between groups for a given comparison.

The computation of principal functional connectivity across the results of the five groups that were shown in Fig. 4 indeed demonstrates that in the delta frequency band (Fig. 5A), initial rest versus meditation showed decreased connectivity between right anterior and left

posterior regions, while final rest versus meditation showed decreased connectivity between left anterior and right posterior regions. In the beta-2 frequency band (Fig. 5B), on the other hand, the differences between the principal functional connectivities of initial rest versus meditation and final rest versus meditation are small, both principal functional connectivities being midline-near and oriented anterior-posterior.

The repeated measure ANOVA (2 comparisons x 2 frequency bands x 2 mean locations x 3 brain axes) of the five groups' data in Fig. 5 yielded a significant interaction (comparisons x frequency bands x mean locations x axes) at $F(2,8)=12.31$, $p=0.0036$. Separate follow-up ANOVAs for the two frequency bands showed a significant interaction (comparisons x mean locations x axes) for the delta band ($F(2,8)=9.34$, $p=0.0080$) and a trend interaction for the beta-2 band ($F(2,8)=3.12$, $p=0.0998$).

The principal functional connectivities of the two comparisons 'initial rest versus meditation' and 'final rest versus meditation' in the delta band (Fig. 5A) showed the following significant topographic differences in the planned least significant difference tests of the data of the five groups: On the left-right axis, the anterior mean locations of the two principal functional connectivities differed at $p=0.03$ and the posterior mean locations differed at $p=0.0002$. On the anterior-posterior axis, the left mean locations of the two principal functional connectivities differed at $p=0.001$ and the right mean locations differed at $p=0.004$. On the inferior-superior axis, the anterior mean locations of the two principal functional connectivities differed at $p=0.08$.

3.3. Coherence between head surface locations

Of the total of 13680 tests (2 comparisons between conditions, 5 groups, 8 frequency bands, 171 coherences per frequency band) for differences between conditions using head surface EEG coherences, only 72 tests were significant after correction for multiple testing; of these, 3 had higher, 69 lower coherences during meditation than rest. ZA cases outnumbered the other four groups: 64 ZA cases versus a total of 8 for the other four groups.

This contrasts starkly with the results for differences between conditions using lagged intracortical coherence, where 359 of the 13680 tests were significant after correction for multiple testing and where, as reported above, all of them revealed lower values, none of them higher values during meditation than rest.

The extremely small number of significant differences in conventional EEG coherence between head surface locations after correction for multiple testing in the four groups LA, QG, SY and AY precluded comparisons with lagged intracortical coherences. In order to meaningfully compare the two analysis approaches, we therefore examined differences of coherence between conditions that reached $p<0.05$ without correction for multiple testing.

Conventional head surface EEG coherence (Fig. 6) clearly showed much greater numbers of lower than higher coherence during meditation compared to rest, initial as well as final. But, there were also notable differences between groups where for example SY and ZA showed more increases than decreases in the theta band for the comparison of initial resting versus meditation (Fig. 6A and B). Across the five groups, the smallest number of lower coherences during meditation versus rest occurred in the theta frequency band (Fig. 6C and D).

Lagged intracortical coherence, on the other hand, at uncorrected $p<0.05$ still yielded only 2 cases of higher coherence during meditation than rest (Fig. 7), but extremely great numbers of coherences lower during meditation than rest, up to 170 of the possible 171 cases per group, comparison and frequency band, particularly great for delta and beta-2 frequencies (Fig. 7A and B).

Fig. 7C and D show that the five traditions displayed some agreement, with the greatest numbers of lower coherences during meditation than rest in the delta and beta-2 frequency band, and the smallest numbers in the alpha-1 band. This latter observation is in contrast to the head surface EEG coherence results of Fig. 6 where the theta band showed the smallest mean number across groups of lower coherences during meditation than rest.

3.4. The magnitude of coherence values

The mean values of all lagged intracortical coherences across the five groups and the three conditions are illustrated in Fig. 8A. Delta, beta-3 and gamma band mean values were very low ($r < 0.02$), while the two alpha bands had the highest mean values ($r = 0.21$, 0.18 , respectively). Comparable distributions occurred in the three conditions (Fig. 8B and C).

The coherence values during rest compared to meditation showed very large differences in some frequency bands, during rest up to 172% of the meditation value (Table 3).

The mean values of lagged intracortical coherence were between 9% (for delta) and 50% (for alpha-1) of the mean values for head surface EEG coherence (Fig. 8A).

Table 3.

Mean coherence values across groups during the two rest conditions expressed as percentages of the values during meditation, and mean coherence values and their standard error (SEM) during the three conditions, for the eight frequency bands.

	Coherence during		Mean coherence (r) across the 5 groups					
	initial rest	final rest	initial	meditation	final	initial	meditation	final
	referred to meditation		rest	meditation	rest	rest	meditation	rest
	%	%	r	r	r	r SEM	r SEM	r SEM
Cortical source regions of interest, lagged coherence								
delta	128	162	0.019	0.015	0.025	0.001	0.004	0.004
theta	102	112	0.064	0.062	0.070	0.006	0.010	0.005
alpha1	109	108	0.215	0.196	0.212	0.047	0.049	0.035
alpha2	134	131	0.194	0.146	0.190	0.037	0.035	0.035
beta1	136	150	0.035	0.025	0.038	0.005	0.004	0.005
beta2	172	162	0.043	0.025	0.041	0.003	0.004	0.002
beta3	150	149	0.019	0.013	0.019	0.003	0.003	0.002
gamma	158	126	0.023	0.014	0.018	0.004	0.003	0.003
Head surface data, conventional coherence								
delta	102	106	0.212	0.208	0.221	0.007	0.005	0.006
theta	98	101	0.257	0.262	0.265	0.007	0.012	0.008
alpha1	109	107	0.431	0.395	0.423	0.037	0.043	0.030
alpha2	117	111	0.418	0.358	0.398	0.034	0.038	0.036
beta1	113	110	0.227	0.201	0.222	0.011	0.015	0.008
beta2	119	111	0.216	0.182	0.201	0.010	0.011	0.009
beta3	109	105	0.167	0.152	0.160	0.003	0.008	0.005
gamma	109	100	0.149	0.137	0.136	0.004	0.013	0.005

3.5. Power spectra

The five groups displayed drastic differences in relative power from each other, but with comparable patterns for initial (Fig. 9A) and final rest (Fig. 9B) compared to meditation, i.e. mean results across groups for initial and for final rest compared to meditation were quite comparable, showing lower values in the alpha-2 frequency band, and higher values in the beta-3 and gamma band (Fig. 9C). During meditation compared to resting, the grand mean values across groups were significantly lowered in the alpha-2 frequency band, and showed a tendency to higher values in the beta-3 and gamma band (Fig. 9D).

4. Discussion

In meditators of five different traditions, the functional connectivity between brain regions coherence was significantly (corrected for multiple testing) lower during meditation compared to rest before meditation as well as compared to rest after meditation. There was not a single case of higher coherence during meditation than rest in any of the five groups and any of the eight frequency bands. This main result was obtained with an analysis strategy (lagged intracortical coherence) that used EEG source modeling to exclude ambiguity of localization and reference-dependence, and that omitted zero phase angle coherences to avoid undue inflation of coherence by volume conduction. Conventional head surface EEG coherence of our dataset also yielded a remarkable predominance of decreased coherence. But, there was also some increased coherence during meditation compared to initial rest (before meditation) and final rest (after meditation).

The reduction of lagged intracortical coherence during meditation was observed in all eight EEG frequency bands, hence similarly concerned inhibitory and excitatory brain functions, e.g. delta and beta frequencies, respectively (Niedermeyer and Lopes da Silva, 2005).

Increase of head surface EEG coherence reportedly is associated with successful task performance (e.g. Anokhin et al., 1999; Beaumont et al., 1978; Holz et al., 2008; Okuhata et al., 2009; Weiss et al., 2005), but also, increased coherence has been reported during sleep compared to wakefulness (e.g. Dumermuth et al., 1983; Kaminski et al., 1997; Nielsen et al., 1990). Thus, the global decrease of coherence during meditation in all our five groups suggests that meditation is not simply comparable to task execution or sleep. We note that neither increase nor decrease of EEG coherence is a virtue in itself; general high coherence is observed during epileptic seizures (e.g. Milton and Jung, 2003) while decreased coherence is observed during schizophrenic symptomatology (e.g. Pascual-Marqui et al., 2011).

Since coherence assesses the cooperativity between system units, lower coherence implies higher functional independence of the system units. Thus, such a finding is expected to result in higher measures of dimensionality. In fact, in a pilot study where we computed Omega dimensionality (Wackermann, 1996, 1999) of our dataset (Faber et al., 2011), three of the five groups showed significant differences between meditation and rest, with higher dimensionality during meditation.

Papers on EEG coherence during meditation analyzed head surface data that in our study showed not only decreased but also increased connectivities. Increased head surface coherence during Transcendental Meditation (TM) has been reported repeatedly as reviewed in the introduction. Unfortunately, our data do not include TM practitioners. Unlike the five traditions in our study, instructions for TM discourage attention to body sensations such as e.g. attention to one's own breathing. We note, however, that one of our groups (QG) also showed increased head surface alpha-1 coherence. Increased head surface alpha coherence was also observed in Zen meditation, but in novices where it is questionable whether they reached optimal states in view of their lack of experience (Murata et al., 2004). Our experienced ZA group did not show increased alpha coherence. The reported increased head surface theta coherence in Sahaja Yoga meditators (Aftanas and Golocheikine, 2001) was also observed in our Sahaja Yoga group (Fig. 6). The increased head surface gamma frequency band phase locking observed in Buddhist meditators (Lutz et al., 2004) suggested increased connectivity; however, our corresponding group of Buddhist meditators generally showed more decreases than increases of head surface EEG coherence during meditation, including the gamma band. Because of the caveats on head surface EEG coherence reviewed in the introduction, conclusions about true functional connectivity remain ambiguous.

Therefore, the present study centered on functional connectivity as measured with intracortical lagged coherence; this approach revealed quite similar results in the five examined, different meditation traditions. We are aware that in other EEG measurements, different meditation techniques are known to show different characteristics (e.g. Dunn et al., 1999; Lehmann et al., 2001; Lutz et al., 2008; Travis, 2001; Travis and Shear, 2010). Also within the framework of the present analysis, the five groups showed clear differences in the frequency of cases of significantly decreased connectivities (Fig. 2A and B). However, the present study did not analyze other specific differences between groups. Our present results demonstrate a major commonality across the five analyzed groups which differed to some extent in practices and experience: In all five separately analyzed groups, intracerebral source model connectivity was lower during meditation than during resting before and after meditation, with relatively small variance of the grand means across groups. Low variance across groups was also evident in the topography of the principal functional connectivities between intracortical ROIs.

Going into and coming out of meditation was associated with different changes of coherence topography in the delta frequency band: In other words, going out of meditation into final rest (after meditation) did not simply reverse the coherence decrease that was observed comparing initial rest (before meditation) with meditation. Thus, the brain breaks up into more independent behavior when going into meditation, and rewires itself when leaving meditation, but via a different route. This is not surprising since one could reasonably expect some temporarily persisting effect of meditation (see also Northoff et al., 2010 on pre-task and post-task resting). Indeed, even long-term electrophysiological effects of meditation are known (Davidson et al., 2003; Lutz et al., 2004; Tei et al., 2009). But, the dissimilarity of the ‘into’ and ‘out of’ changes of connectivity was surprising: The topographies of the two principal connectivities were about orthogonal to each other. When going into meditation, there was a diagonally oriented right anterior to left posterior decrease of connectivity; coming out of meditation, there was also a diagonally oriented but crossed increase of connectivity oriented left anterior to right posterior. On the other hand, the beta-2 frequency band largely showed a reversal of connectivities: both the in- and out topographies of the principal connectivities were midline-near, and anterior-posterior oriented, showing only small location differences. The remarkable diagonal orientation of the delta band principal connectivities is reminiscent of the observation that no-task resting EEG activity when clustered into four classes of spatial configurations of the brain electric field yields two classes with clearly diagonal oriented brain electric axes that cover about 50% of the total analysis time (Britz et al., 2010; Koenig et al., 2002).

The results of our study show, in sum, that functional interdependence between brain regions is globally reduced in optimal meditation states, regardless of the followed specific meditation practices, and that this reduction concerns inhibitory as well as excitatory brain activities. This increased functional independence – the decreased cooperativity - of brain processes suggests that experiences are handled more independently and influence less each other and the self process with its conscious experience. The self process comprises functions such as self awareness, autobiographic memory, agency, and embodiment (see e.g. Blanke and Arzy, 2005; Conway, 2005; Esslen et al., 2008; Farrer and Frith, 2002; Jantz and Beringer, 1944; James, 1890).

How may the observed general reduction of functional connectivity explain the major subjective experiences during meditation: On one hand the non-involvement of the self in momentary thoughts or percepts, and on the other hand the expansion of self consciousness (Cahn and Polich, 2006)? We propose the following speculative explanation: Because of the reduced internal connectivity of the functions of the self process, their processing of information coming from other processes is curtailed; this leads to a subjective experience

which is described for example as non-involvement, detachment, and letting go. On the other hand, because the diminution of information handling within the self process progressively deprives the self process of constraining information about external and internal realities, this leads to a subjective experience which is described for example as expansion of consciousness, dissolution of ego borders, and all-oneness. Future work will have to examine possible specifics of these theories.

Acknowledgment

The authors thank Prof. Hiroaki Kumano for helpful discussions and Marlene E. Steiner, M.A. for work in data collection. Supported in part by Grant Nr. 44/06 from the Bial Foundation, S. Mamede do Coronado, Portugal.

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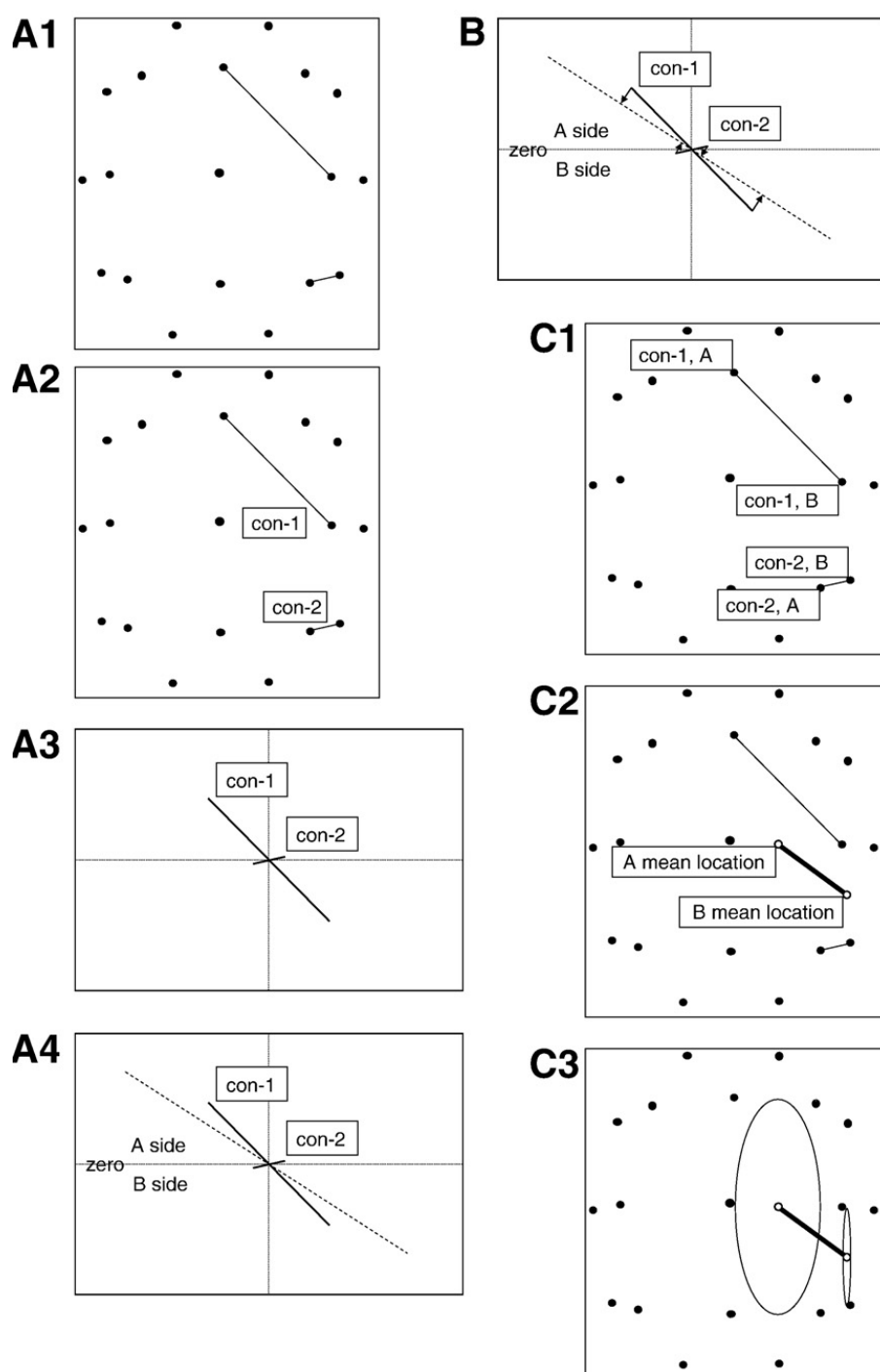


Fig. 1. Computation scheme of the ‘principal functional connectivity’. Head seen from above, nose up. A1, A2: ROIs shown as dots in glass brain view; presume there are two significant connectivities (con-1, con-2, shown as straight lines), each one joining two ROIs. A3: The connectivities were centered by subtracting for each pair of joined ROI locations the mean location of the pair. A4: Presume the first principal component computed in 3-dimensional space for the two participating location pairs (connectivities) yields the dashed straight line, corresponding to the principal direction of the connectivities. B: The significant connectivities are projected onto the principal component straight line and the locations are labeled as “A” (for the positive projection) and “B” (for the negative projection). C1: The labeled ROIs of the significant connectivities shown in the original space. C2: The original pair locations of the participating connectivities, now labeled as A and B, are separately averaged for A’s and B’s, giving the mean locations thus constituting a principal functional connectivity. C3: Mean locations and standard errors of the principal functional connectivity resulting from the two significant connectivities shown in A1.

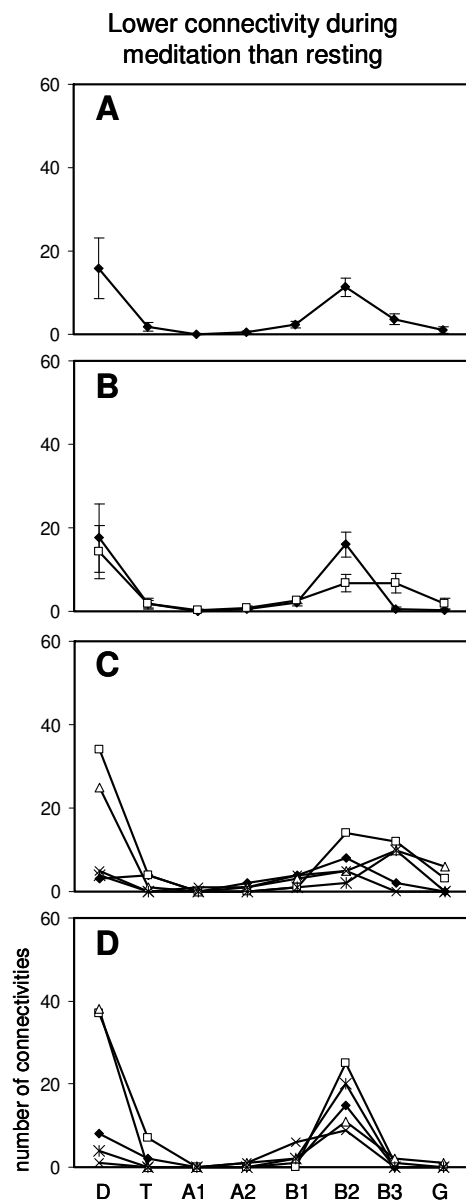


Fig. 2. Numbers of connectivities between intracortical ROI's (assessed with intracortical lagged sLORETA-based coherence) that differed significantly between meditation and rest after correction for multiple testing. Note that all significant cases had lower coherence during meditation than rest, i.e. there was no significantly different case with higher intracortical lagged coherence during meditation than rest. A: Initial rest versus meditation, and B: final rest versus meditation, displaying the total number of significant cases for each of the five groups. C: Mean number of significant cases (and S.E.) across the five groups for meditation versus initial rest (i-R) and meditation versus final rest (f-R). - D: Grand mean number of significant cases (and standard error) across the five groups, for meditation versus mean of initial and final rest. - EEG frequency bands: D=delta; T=theta; A=alpha; B=beta; G=gamma.

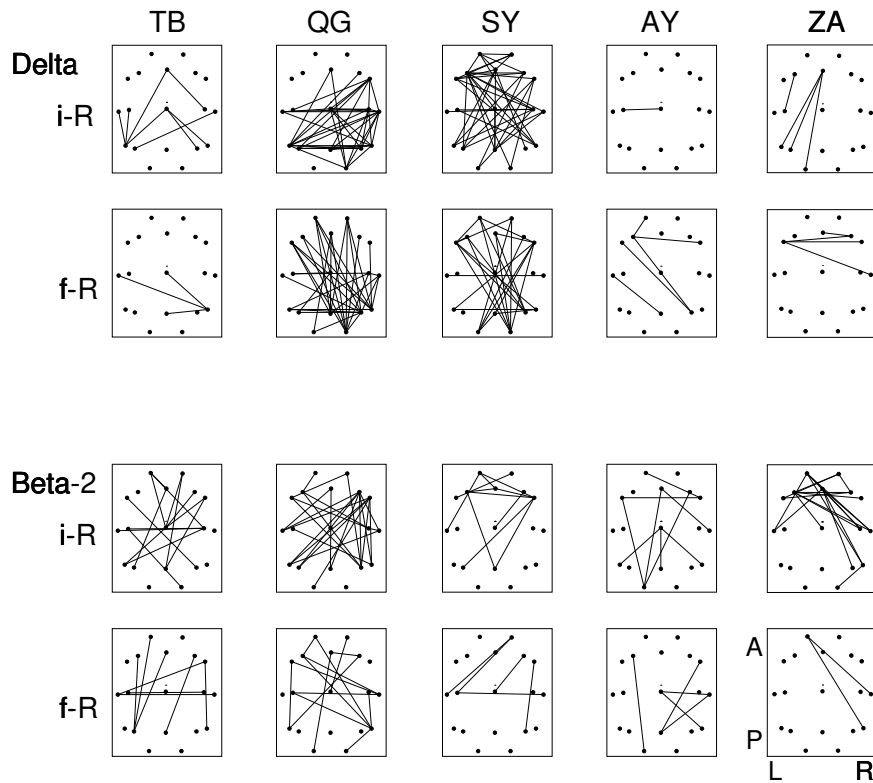


Fig. 3. Glass brain views of connectivities (in the delta and beta-2 frequency bands) that were significantly different (corrected for multiple testing) between initial rest (i-R) versus meditation, and final rest (f-R) versus meditation, in the 5 groups. Note that all significant connectivities were lower in meditation than rest. TB: Tibetan Buddhists, QG: QiGong, SY: Sahaja Yoga, AY: Ananda Marga Yoga, ZA: Zen. The 19 ROIs are indicated by dots. Head seen from above, nose up. A: anterior, P: posterior, L: left, R: right.

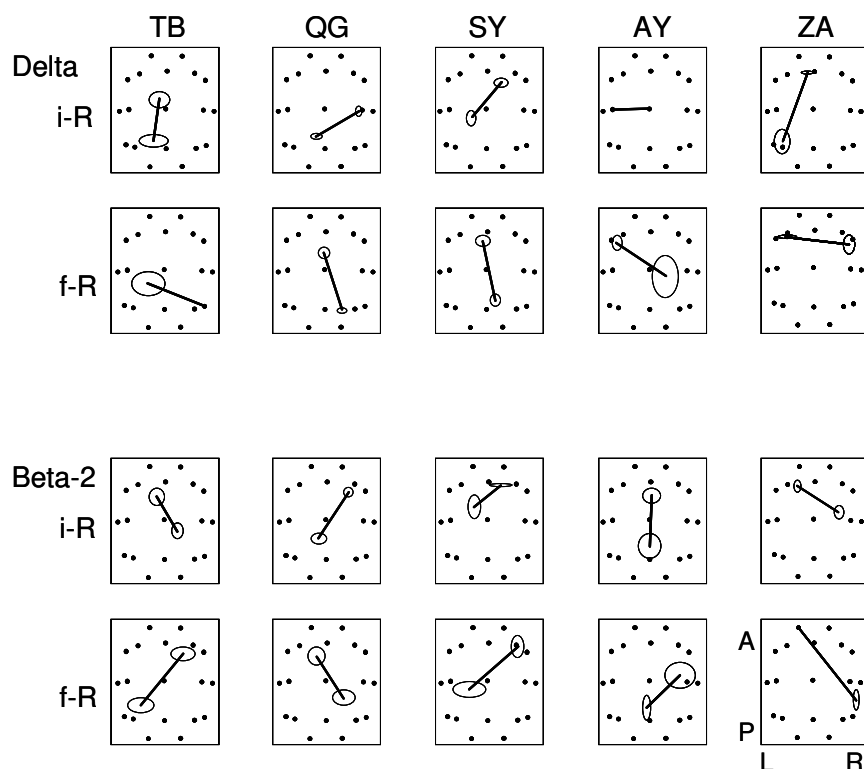


Fig. 4. Glass brain views of principal functional connectivities computed from the results in Fig. 3 for each of the five groups. The mean locations of the principal functional connectivities and their standard error (round shapes) of the means across the five groups are displayed. TB: Tibetan Buddhists, QG: QiGong, SY: Sahaja Yoga, AY: Ananda Marga Yoga, ZA: Zen. i-R: Meditation versus initial rest; f-R: Meditation versus final rest. The 19 ROIs are indicated by dots. Head seen from above, nose up. A: anterior, P: posterior, L: left, R: right.

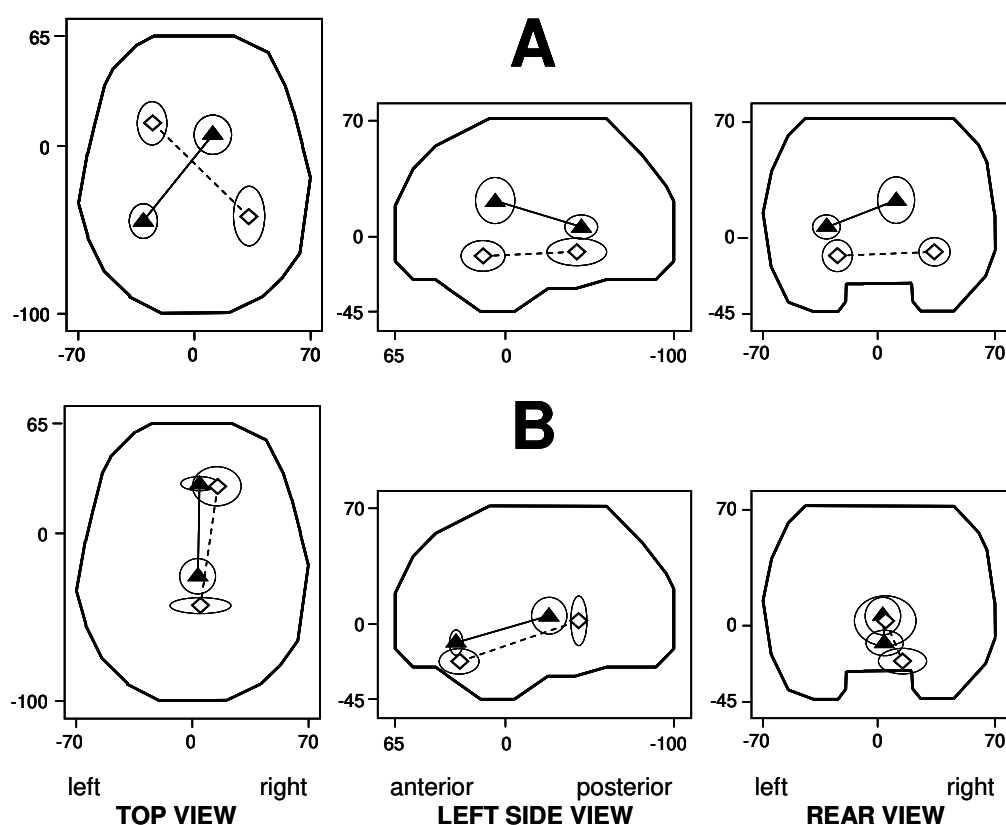


Fig. 5. Principal functional connectivities in the delta (A) and beta-2 (B) frequency band. Means (symbols) and standard errors of the mean localizations (round shapes) of the principal functional connectivities of decreased lagged intracortical coherence across the five groups. Black triangles: initial rest versus meditation; Open diamonds: final rest versus meditation. Glass brain views. Axis scales correspond to millimeters in the digitized Talairach atlas from the Montreal Neurological Institute. Note the small variance of the mean localizations across groups.

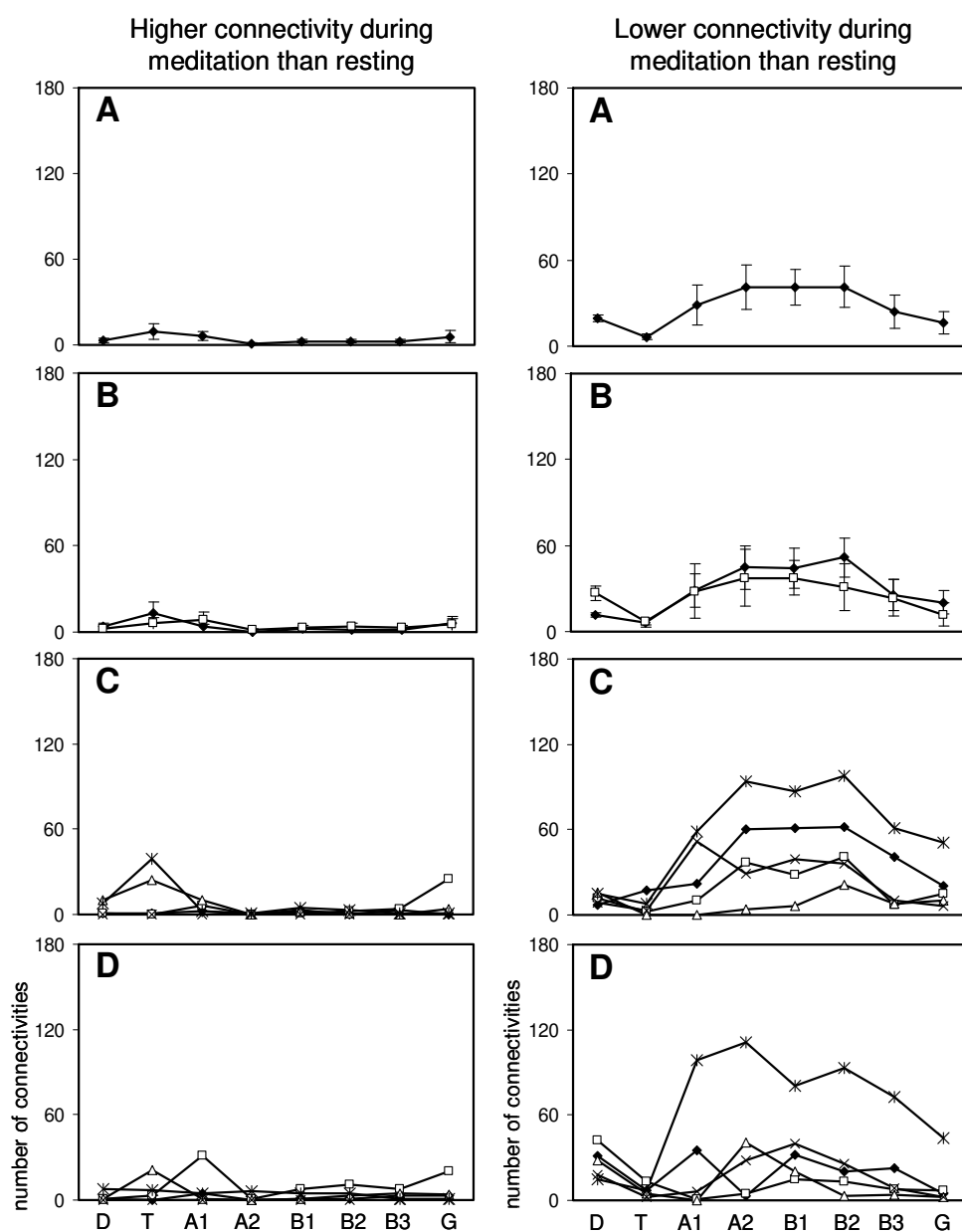


Fig. 6. Number of head surface EEG connectivities between electrode positions that changed in intensity at $p(\text{uncorrected}) < 0.05$ between initial rest versus meditation and final rest versus meditation. Left: cases of increased connectivities; Right: cases of decreased connectivities. A: Number of connectivities in each of the five groups, initial rest versus meditation. B: Number of connectivities in each of the five groups, final rest versus meditation. C: Mean across groups, initial rest versus meditation (solid symbols) and final rest versus meditation (open symbols), and standard errors of the means. D: Grand mean (and standard error) across the five groups (mean of initial and final rest versus meditation). – EEG frequency bands: D=delta; T=theta; A=alpha; B=beta; G=gamma.

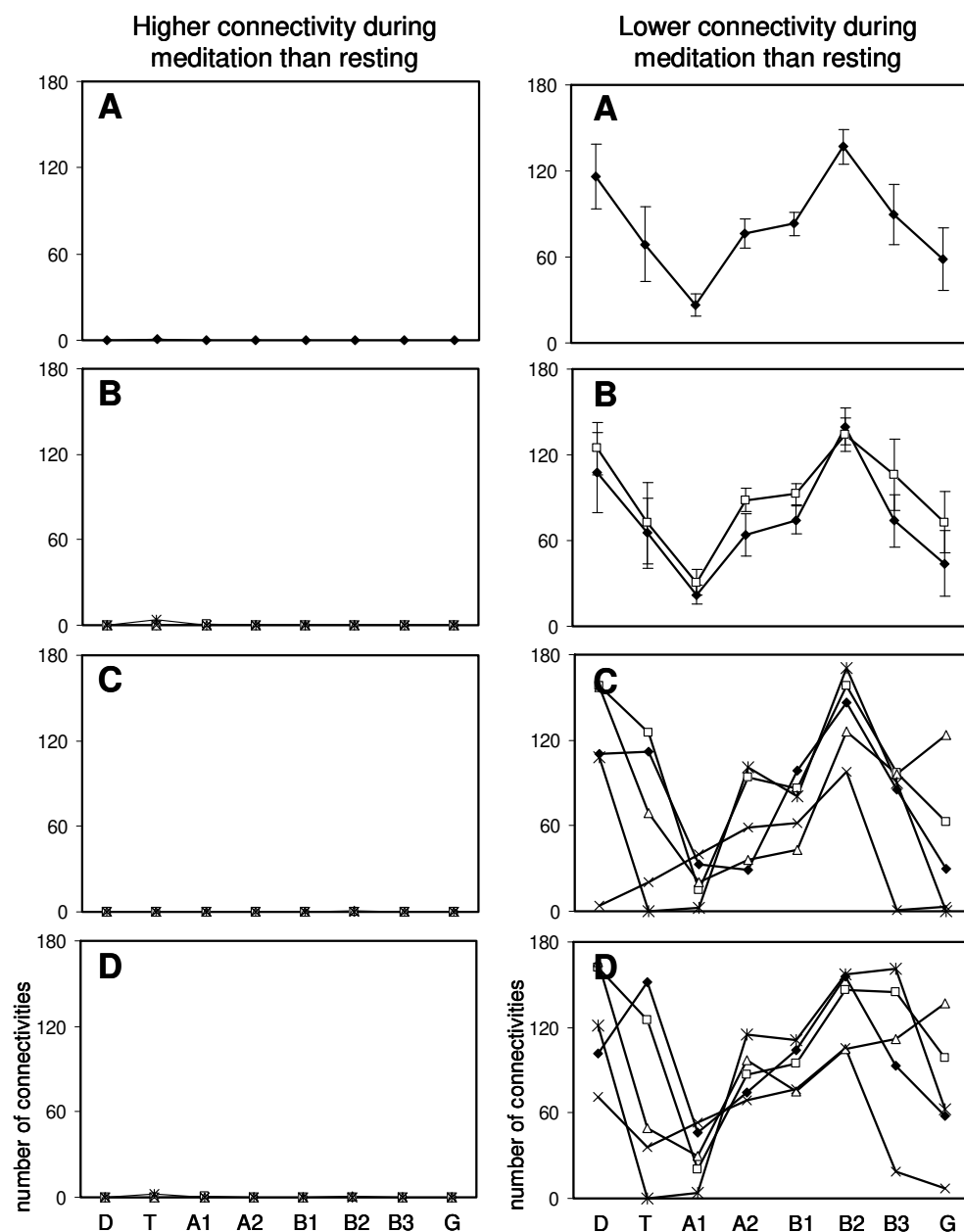


Fig. 7. Number of lagged intracortical connectivities between ROIs that changed in intensity at $p(\text{uncorrected}) < 0.05$ between initial rest versus meditation and final rest versus meditation. Left: cases of increased connectivities; Right: cases of decreased connectivities. A: Number of connectivities in each of the five groups, initial rest versus meditation. B: Number of connectivities in each of the five groups, final rest versus meditation. C: Mean across groups, initial rest versus meditation (solid symbols) and final rest versus meditation (open symbols), and standard errors of the means. D: Grand mean (and standard error) across the five groups (mean of initial and final rest versus meditation). - EEG frequency bands: D=delta; T=theta; A=alpha; B=beta; G=gamma.

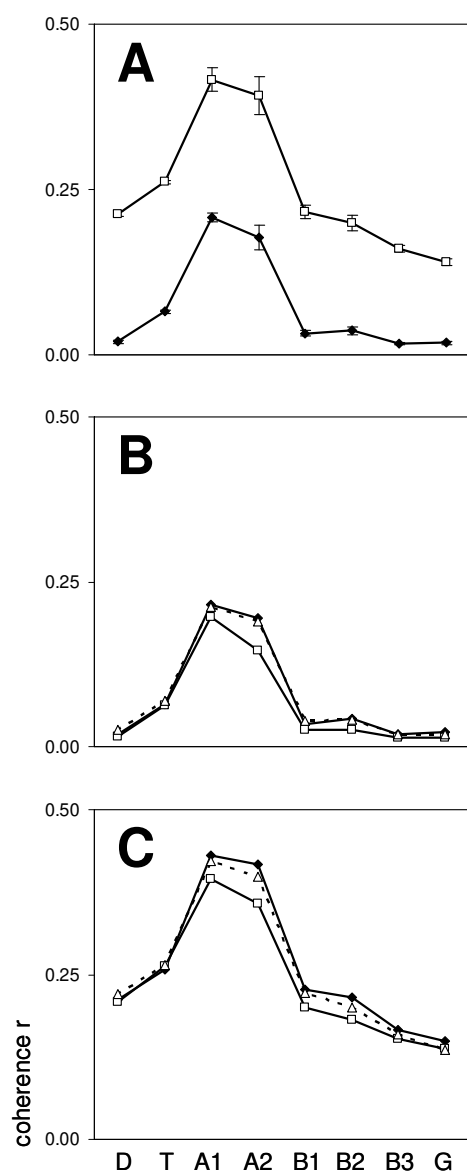


Fig. 8. A: Mean values of coherence and standard error of the mean across the five groups in the eight EEG frequency bands. ROIs: lagged intracortical coherence between ROIs; EEG: head surface EEG coherence. - B: Lagged intracortical coherence between ROIs, and C: Head surface EEG coherence values, averaged across groups. i-R: initial rest; f-R: final rest; meditation. - EEG frequency bands: D=delta; T=theta; A=alpha; B=beta; G=gamma.

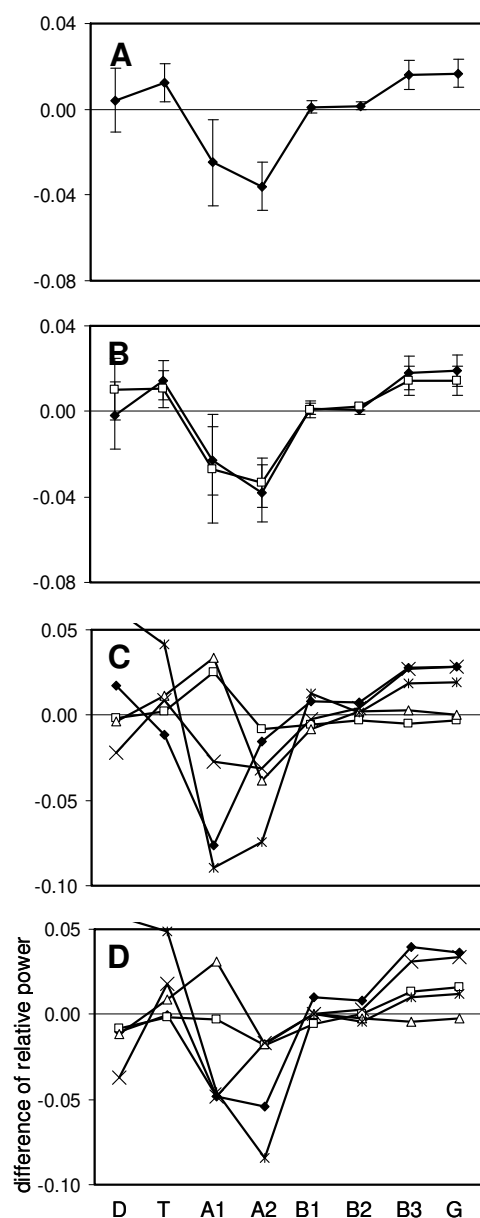


Fig. 9. A: Mean differences of relative power during meditation minus initial rest of the five groups. B: Mean differences of relative power during meditation minus final rest of the five groups. C: Mean differences of relative power across groups and standard error of the mean during meditation minus initial rest (closed symbols) and during meditation minus final rest (open symbols). D: Grand mean differences of relative power across groups (and standard error) during meditation minus mean rest in the eight EEG frequency bands. - EEG frequency bands: D=delta; T=theta; A=alpha; B=beta; G=gamma.